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Variation in the species richness of parasitoid wasps (Ichneumonidae: Pimplinae and Rhyssinae) across sites on different continents

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Running title: Species-richness patterns in parasitoid wasps

ABSTRACT

1 The old idea that parasitoid wasps (Ichneumonidae) show an inverse latitudinal diversity gradient has recently been challenged, but how ichneumonid species richness varies across the globe is still not well understood. We carried out field inventories in 21 sites on three continents to clarify this question, focusing on the subfamilies Pimplinae and Rhyssinae. Our total sampling effort was 628 Malaise trap months and the total catch exceeded 65,000 individuals. Our main focus was in two intensively inventoried areas in Amazonia, together yielding 257 Malaise trap months and 26,390 ichneumonid individuals.

2 To expand the scope and assess global species diversity patterns of the Pimplinae and Rhyssinae, we compiled published species lists from a total of 97 study localities around the world. The highest observed species richness in any locality, 105 species, was found in one of our field sites in Peruvian Amazonia. None of the other localities reported more than 70 species, even the ones with a sampling effort comparable to ours.

3 Despite the local thoroughness of our field inventories in Amazonia, data analyses indicated that a substantial proportion of the parasitoid wasp species occurring in each site remained unobserved.

4 The highest local species richness values were reported from the tropics. However, parasitoid wasps are still too sparsely sampled to draw solid conclusions about whether or not their species richness follows a particular latitudinal trend, and if so, where their richness peaks.

Key words. Amazonia, biodiversity, biogeography, latitudinal gradient, Peru, Pimplinae, rain forest, Rhyssinae.

INTRODUCTION

The parasitoid wasp family Ichneumonidae is the most species-rich hymenopteran family, and it is among the most diverse animal groups on Earth. Interestingly, it has been suggested that the Ichneumonidae is less species-rich in tropical regions than at higher latitudes, i.e. that the family presents an inverse latitudinal diversity gradient (e.g. Owen & Owen, 1974; Timms *et al.* 2015). Over the years, various hypotheses have been proposed to explain why ichneumonids are relatively species-poor in the tropics (Santos & Quicke, 2011). However, the high number of newly described taxa in recent taxonomic publications shows that tropical ichneumonids are still incompletely known (e.g. Aguiar & Ramos, 2011; Broad *et al*., 2011; Santos & Aguiar, 2013). Therefore, further large-scale and long-term studies are needed, especially in the tropics, to improve our knowledge about global ichneumonid diversity patterns.

Amazonia is the largest rainforest area in the world, but also one of the least known in terms of its insect fauna. Although western Amazonia is famous for its high diversity in several animal and plant groups (Gentry, 1988, 1992; Robins, 1996; Robbins & Opler, 1997; Patterson *et al.,* 2006), some early authors proposed that ichneumonid diversity is low in Amazonia (Porter, 1978). These studies were based on small data sets, and the situation has changed in the 2000s, as new studies on Amazonian ichneumonid diversity have challenged the old paradigm (Sääksjärvi *et al*., 2004; Gómez *et al*., 2015; Veijalainen *et al*., 2013).

In this study, we compare observations of local species richness of pimplines and rhyssines across latitudes on the basis of field sampling we carried out in 21 sites on three continents. The two most intensively studied areas were in Peruvian Amazonia, where the sampled localities were selected so as to span different forest types (Sääksjärvi *et al*., 2004; Goméz *et*

al., 2014, 2015). Most sampling was done with Malaise traps, but in the two Peruvian areas, we also used other sampling methods for comparison.

The main aims of this study are 1) to document how species accumulation of pimpline and rhyssine wasps relates to sampling effort in our two well-sampled Amazonian sites, and 2) to assess global patterns in pimpline and rhyssine species richness using data from both our own inventories and from publications of other researchers.

MATERIAL AND METHODS

STUDY ORGANISMS.—The parasitoid wasp family Ichneumonidae currently includes about 40 subfamilies, 1,600 genera and 24,000 described species (Aguiar *et al*., 2013), making it the most species-rich family within Hymenoptera. Here we focus on two of the most extensively studied subfamilies in the Neotropical region, Pimplinae and Rhyssinae (e.g. Porter, 1978; Gauld, 1991; Gauld *et al*., 1998, 2002; Sääksjärvi *et al*., 2004; Gómez *et al*., 2009, 2014, 2015; Gómez & Yabar, 2015).

The subfamily Pimplinae is a relatively large, cosmopolitan group with about 78 genera (Pham, 2013) and more than 1,500 described species worldwide (Yu *et al*., 2012). This is the most biologically diverse of all ichneumonid subfamilies and it is associated with a wide range of hosts (Gauld, 1991). The species are mainly idiobiont ectoparasitoids of immature stages of holometabolan insects or idiobiont endoparasitoids of lepidopteran or hymenopteran pupae. However, the species of the *Polysphincta* genus-group are koinobiont ectoparasitoids of immature and mature spiders (Gauld & Dubois, 2006).

The subfamily Rhyssinae is a relatively small, cosmopolitan group with eight genera worldwide and more than 250 described species (Gómez *et al.*, 2015). According to Kamath & Gupta (1972), the species-richness of Rhyssinae is highest in the lowland rainforests of South-East Asia. In the Neotropical region the species are believed, on the basis of the known biology of a few Old World species, to be idiobiont ectoparasitoids of immature stages of endopterygote insects boring in wood (Gauld, 1991).

STUDY SITES.— We carried out intensive long-term sampling in two sites in Peruvian Amazonia, Allpahuayo-Mishana in the north and Los Amigos in the south. In addition, we sampled 19 sites outside Amazonia. The distribution of these sites is shown in Fig. 1. Elevation, geographical coordinates and sampling effort of each locality are given in Supplementary materials (Table S1).

Allpahuayo-Mishana National Reserve (3° 57-58' S, 73° 25-26' W) is located in northern Peruvian Amazonia in the department of Loreto. The climate is tropical, with mean annual precipitation of about 3000 mm and mean annual temperature of 26 °C (Marengo, 1998). Elevation is between 100 and 180 m above sea level and the prevailing vegetation is moist tropical forest according to the Holdridge (1967) classification. The environmental conditions have been described in Kalliola & Flores Paitán (1998). Our ichneumonid sampling was carried out in non-inundated areas (*terra firme*), where the terrain is divided among three main soil types. Flat low-lying areas often have soils derived from the marine Pebas formation of Miocene age. These soils are clayey in texture, relatively rich in nutrients, and mostly brownish-grey in colour (Kalliola & Flores Paitan, 1998). The tops of the plateau-like hills often have white sand soils, which are nutrient-poor and white or grey in colour. Loamy soils are probably derived from old river terraces (Kalliola & Flores Paitan, 1998). The

forests growing on the clayey to loamy soils have a classical rain forest physiognomy with large trees and different canopy layers, whereas the white sand forests have slenderer trees and a less complex canopy structure (Anderson, 1981; Tuomisto & Ruokolainen, 1994).

Los Amigos Conservation Concession (12° 33-34'' S, 70° 04-05' W) is located in the southern Peruvian Amazonia in the department of Madre de Dios close to the Andean-Amazonian interface. Mean annual precipitation is about 2 770 mm and annual mean temperature 23 °C with monthly mean temperatures varying 20-26 °C (Gómez, 2009). This is somewhat drier, cooler and more seasonal than in Allpahuayo-Mishana. Elevation varies between 230 and 270 m above sea level and the vegetation is moist tropical forest according to the Holdridge (1967) classification. For description of the environmental conditions, see Wilson & Sandoval (1996). The Los Amigos watershed comprises sediments dated from the Neogene and Quaternary that have been deposited during the last 20 million years (Pino, 2007). Due to the proximity of the Andes, the soils are a mosaic of clayey, sandy, silty and gravelly materials, but extremely nutrient-poor soils such as white sands have not been reported for the area. Our ichneumonid sampling covered both non-inundated and seasonally inundated forests. In general, *terra firme* soils are sandier, more acidic and poorer in nutrients than those located in the floodplains (Hovikoski *et al*., 2005).

Seven of our other 19 sampling localities are located in temperate South America between the regions of Maule (35°S) and Los Lagos (42°S) in Central Chile. One sampling locality is in Central America on Coiba island off the Pacific coast of Panama (7°N). This is a national park and the vegetation is moist tropical forest according to Holdridge's classification. Eight sampling localities were established in the temperate region of Spain, between 38°N and 42°N; for details see Nieves-Aldrey (1995).

Three localities are situated in the Canary Islands in Isla de la Palma (28°N) and were mostly dominated by forests of the endemic Canarian pine (*Pinus canariensis* Chr. Sm. ex DC; for survey details see Domingo Quero *et al*., 2003). One sampling locality is in central Africa, the Kibale National Park in Uganda.

SAMPLING METHODS.—Our primary sampling method consisted of long-term Malaise trapping. A Malaise trap is an open tent-like structure widely used in entomological studies, and ichneumonid surveys in particular, because it is efficient in collecting insects that are strong flyers (Nieves-Aldrey & Rey del Castillo, 1991, Sääksjärvi *et al*., 2004; Mayhew *et al*., 2009). Thanks to the popularity of Malaise traps, it was possible to find comparable data from earlier parasitoid studies, as the sampling effort can be conveniently expressed in terms of Malaise trap months (MTM). One MTM corresponds to one trap collecting in the field for a period of one month (or a combination of more traps that cumulatively operate for one month).

In the Peruvian Allpahuayo-Mishana, we combined data from three separate field campaigns. The first one ran from August 1998 to January 1999 with 12 traps and had a total sampling effort of 41 MTM. The second ran from January 2000 to January 2001 with 15 traps and had a total sampling effort of 144 MTM. Both of these campaigns have been described by Sääksjärvi *et al*. (2004). The last campaign was conducted by 14 Malaise traps, four of which were active in April-December 2011 and ten in October-December 2011. The total sampling effort of these traps was 45 MTM, and details have been described by Gómez *et al*. (2015). In Los Amigos, nine Malaise traps were in operation in May-July 2008 with a total sampling effort of 27 MTM. The total sampling effort in Allpahuayo-Mishana and Los Amigos

combined was 257 MTM. To our knowledge, this is the most extensive sampling of ichneumonids in Amazonia.

To find out if Malaise trapping might be systematically biased and miss some species entirely, we applied four additional sampling methods in Allpahuayo-Mishana and one in Los Amigos (Table 1) 1) Yellow pan traps (Moericke traps). During 23 weeks, a total of 100 traps were set out in Allpahuayo-Mishana for a period of 24 hours every week. In each weekly sampling, the traps were spread across the different forest types. 2) Hand netting with a standard entomological net. This was done weekly for 13 weeks in Los Amigos and for 23 weeks in Allpahuayo-Mishana. Each netting session consisted of four hours of random sweeping in the vegetation of different forest types. 3) Larval rearing. A total of 3,298 lepidopteran larvae were collected in the forests of Allpahuayo-Mishana and reared individually in one-litre plastic jars. 4) Pupal rearing. A total of 113 lepidopteran pupae were collected in the forests of Allpahuayo-Mishana and reared individually in one-litre plastic jars.

The number of localities and sampling effort outside Amazonia is as follows: seven in Central Chile (45.4 MTM), one in Panama (1.4 MTM), seven in Spain (57.4 MTM), three on the Canary Islands (4.8 MTM) and one in Uganda (252 MTM). Samples from all localities were prepared and identified in the Zoological Museum of the University of Turku (ZMUT) and the National Museum of Natural Sciences, Madrid (CSIC).

GLOBAL COMPARISON OF PIMPLINAE AND RHYSSINAE SPECIES-RICHNESS.—To evaluate global patterns in Pimplinae and Rhyssinae species richness we searched the literature for ichneumonid inventories that could be compared with our field data. Because the number of observed species is dependent on sampling effort, we only considered quantitative inventories that had used Malaise traps and in addition recorded the duration of sampling and/or the number of captured Pimplinae and Rhyssinae individuals. We found 76 studies fulfilling these criteria. In most cases, relevant information for our analysis was not available in the original publication but was kindly provided by the authors of the studies (see Table S1).

All the inventories were carried out in delimited sites with little altitudinal variation. In most cases, the variation within a locality was less than 200 meters. It was important to ensure that all data points represented single localities; if some had included longer altitudinal gradients than others, drawing conclusions about latitudinal patterns in local species richness would not be appropriate. Some published inventories only included data on the subfamily Pimplinae. Because this subfamily is much more abundant and species-rich than Rhyssinae (Gauld, 1991) we used these data as well but identify them in the results.

DATA ANALYSIS.—Our first aim was to document species accumulation patterns as a function of sampling effort in the Peruvian sites, for which time series data were available. Each sampling interval (originally 1 or 2 weeks) from each trap was used as a separate sampling unit. Species accumulation curves were obtained in two different ways. Firstly, the actual observed species accumulation was documented by aggregating consecutive sampling intervals from the beginning of a trap's operation to its end. Secondly, sampling units were combined in a random order, within habitat types only, to observe patterns of species accumulation at the site level.

To take into account species abundance patterns, we calculated the effective number of species, also known as true diversity. This equals the reciprocal of the weighted mean of the proportional species abundances, with the species abundances themselves used as the weights and the parameter q defining which mean is used (Tuomisto, 2010). We used two different means, the geometric mean (corresponding to q=1) and the arithmetic mean (q=2). The former gives a diversity value that equals the exponential of the well-known Shannon index, and the latter gives a value that equals the inverse Simpson index.

We used the Chao-1 estimator to assess how many additional species could be expected at a site, given the number of species observed only once or twice with a given sampling effort. The estimated number of additional species was then compared with the corresponding sampling effort to check for any indication that species sampling was approaching completeness.

Division of the Peruvian data to subsets of different sampling efforts made it possible to compare richness values from elsewhere in the world with Peruvian data of similar sampling effort. Here we focus on the effect of sampling effort only, and do not take into account possible effects of seasonality. The effect of habitat heterogeneity was minimized by only pooling samples taken in the same forest type. This was done to ensure that the Peruvian species richness values are not inflated in relation to the other sites, for which information on possible habitat heterogeneity was not available. Species accumulation was plotted against both sampling effort in the strict sense (the length of the sampling interval in MTM) and sampling efficiency (the number of Pimplinae and Rhyssinae individuals captured). In addition, we analysed latitudinal and elevational trends in local species richness after taking into account the effect of sampling efficiency. This was done by first fitting a second-order polynomial regression of number of species against number of individuals (both

logarithmically transformed), and then using the residuals from this regression as the response variable in linear regression against latitude or elevation. All analyses were done in the R environment using either the 'vegan' package (Oksanen *et al*., 2013) or code written by HT.

RESULTS

The 21 localities we sampled in different parts of the world produced a total catch of approximately 65,000 ichneumonid individuals, of which 2,698 individuals representing 293 species were Pimplinae or Rhyssinae. In Allpahuayo-Mishana, all sampling methods together yielded a total of 24,378 ichneumonid individuals representing 19 subfamilies. The subfamily Pimplinae was represented by 1,516 individuals (92 species) and the subfamily Rhyssinae by 81 individuals (13 species; Table S2). In Los Amigos, a total of 2,012 ichneumonid individuals representing 18 subfamilies were captured. The subfamily Pimplinae was represented by 106 individuals (42 species) and the subfamily Rhyssinae by 15 individuals (nine species; Table S2).

The two Peruvian sites had 16 genera of Pimplinae, 9 (56%) of which were shared, and a single shared genus of Rhyssinae (Table S2). The species compositions of the two sites were rather different: of the 128 Pimplinae and Rhyssinae species observed, 81 species (63%) were only collected in Allpahuayo-Mishana, 23 species (18%) only in Los Amigos, and only 24 species (19%) were shared between both localities. In other words, the overall similarity of the species compositions in the two sites equaled 0.19 if measured with the Jaccard index and 0.32 if measured with the Sørensen index. It is noteworthy that half of the species that were

observed in Los Amigos were not observed in Allpahuayo-Mishana in spite of the massive sampling effort (230 MTM) in the latter.

In both Peruvian sites, the Malaise trap proved to be the most efficient collecting technique, as all the Pimplinae and Rhyssinae species encountered in the inventory were found in Malaise traps. The other methods only yielded additional individuals of some of the species.

In the 2011 inventory in Allpahuayo-Mishana, Malaise trapping captured 1,961 ichneumonid individuals, which was 74% of the total captured with all methods together in that year (2,640 individuals). Yellow pan trapping yielded 511 ichneumonid individuals (19% of the total) and hand netting produced a catch of 142 individuals (5% of the total). Larval rearing produced 22 individuals and pupal rearing only four individuals. Given that 3,411 lepidopteran larvae and pupae were reared, this indicates that only a small proportion of them were parasitized by ichneumonids.

Overall, Cryptinae was the most abundant subfamily with 1,168 individuals (44% of the total), whereas Pimplinae with 205 individuals and Rhyssinae with 19 individuals represented smaller proportions of the total catch (5% and 0.7%, respectively). The individual Malaise traps differed greatly in how many individuals and species they captured per unit time, but there did not seem to be any systematic trend in this either among habitat types locally or between the two Peruvian sites (Fig. 2A, B). When species accumulation was related to the number of individuals captured, much more uniform trends were observed across the traps. There was only a modest tendency for species accumulation to slow down with increasing sampling efficiency (Fig. 2C).

The Chao-1 estimates indicated that even at the largest sample sizes within habitat types, many species still remained unobserved (Fig. 3). The estimated number of unseen species

was only weakly related to the number of individuals already observed, although a decreasing tendency emerged when the sample size became larger than about 200 individuals. A linearly decreasing trend was found if the estimated number of unseen species was expressed as a percentage of the observed number of species (3B). Nevertheless, even at the largest sample sizes available to us, it was still estimated that the number of species would increase by 10-30% if more individuals were sampled.

The global sampling effort for Ichneumonidae that is both known to us and reports adequate data for comparison (Table S1) totals 3,267 MTM. Costa Rica is the best-studied country with data available from 17 localities with a combined sampling effort of 1,266 MTM (39 % of the world total). Our Peruvian study contributed 19 % of the world total (628 MTM). In general, most of the study sites were at relatively low altitudes with only 10 of the 97 localities (about 10 % of total MTM) occurring above 2000 m elevation.

Our Malaise traps in Peruvian Amazonia were about as efficient in capturing Pimplinae and Rhyssinae individuals as the traps for which results have been reported in the literature: the number of individuals caught with any given number of Malaise traps months in our data was firmly within the limits reported from other sites with a similar number of Malaise trap months (Fig. 4A). In contrast, the number of species caught in the Peruvian traps was generally higher than the numbers of species reported for the same number of Malaise trap months elsewhere (Fig. 4B). This difference became even clearer when the number of species was shown against number of individuals: for any given number of individuals captured, the number of species observed was always highest in the Peruvian samples (Fig. 5A).

All the sites with more than 50 observed species were in the tropics, and the upper limit of local species richness clearly decreased towards the poles. However, sites with very few observed species (even taking into account sampling effort) were found at all latitudes (Fig.

6). Therefore, no consistent overall gradient in species richness could be seen in relation to latitude. With elevation, the relationship was even weaker.

When some species are more abundant than others, the effective number of species (=species diversity) becomes smaller than the actually observed number of species. This effect was clearly visible in our Peruvian data (Fig. 5). Differences between the habitat types in species accumulation were small, but traps in white sand forests tended to yield fewer species for a given number of individuals than traps in the other habitats. Interestingly, the traps in secondary forests tended to have relatively high species richness, but these samples were dominated by a few species, which resulted in clearly decreasing diversity with increasing value of *q*. The species diversity accumulation curves also showed a distinct tendency to level off at a much earlier stage than the species-richness accumulation curve did.

The general impression from plotting observed species richness against latitude was that the highest numbers of species are found in the tropics (Fig. 6A). This impression was confirmed for the lowland sites when the effect of collecting efficiency (number of individuals) was taken into account, but no such trend was seen among the montane sites (Fig. 6B). Within the tropical sites, species richness seemed to decrease with elevation, but no trend was observed in the non-tropical sites (Fig. 6C).

DISCUSSION

PARASITOID WASP SPECIES-RICHNESS.—Allpahuayo-Mishana is currently the site with the highest known species-richness for pimpline and rhyssine wasps in the world, with 105 species. Our current estimate is that 27 of these (25.8%) represent already described species, whereas 78 species (74.2%) are new to science.

The total sampling effort in Allpahuayo-Mishana was 240 MTM, which is high in global comparison (Table S1). However, the most intensively sampled locality in the world known to us is Santa Rosa in Costa Rica, where researchers have observed 40 species with a sampling effort of 576 MTM (Gaston & Gauld, 1993). Only four other sites can boast a sampling effort exceeding 100 MTM for Pimplinae and Rhyssinae, and none of these has reported more than 26 species (Table S1): Cerro Hacha in Costa Rica, Ria Lagartos in Mexico, Cabañeros in Spain and Kibale in Uganda. The two Peruvian localities show consistently higher numbers of Pimplinae and Rhyssinae species than most other sites when comparisons are made among subsamples based on an equivalent sampling effort (MTM; Fig. 4B). The difference becomes even more evident when comparisons are based on sampling efficiency (number of individuals; Fig. 5A).

Peruvian Amazonia is known to have high habitat heterogeneity (Tuomisto *et al*., 1995), and it has very high species-richness of trees (Gentry 1988, 1992), butterflies (Robins 1996, Robbins & Opler, 1997) and birds (Patterson *et al*., 2006).

Pimplinae and Rhyssinae, and idiobiont ichneumonids in general, have already been documented to be species-rich groups in the tropics (Gauld, 1991; Sime & Brower 1998; Quicke, 2012). These subfamilies are among the best-known groups of parasitoids in the Neotropics, but our results indicate that their species richness in Amazonia is even higher than previously reported by Sääksjärvi *et al*. (2004).

Recent findings have demonstrated that the subfamily composition of idiobiont and koinobiont ichneumonids is rather similar in temperate and tropical regions (Veijalainen *et al*., 2013). Furthermore, also high numbers of koinobiont species have been discovered recently from the tropics (Broad *et al*., 2011; Khalaim & Broad, 2013). These findings

together with our results suggest that species richness of both idiobiont and koinobiont ichneumonids is still mainly undiscovered and most likely very high in the tropics.|

The functional composition of the pimpline and rhyssine faunas in our Peruvian Amazonian study localities (Table S2) is rather similar to that in other tropical study localities (e.g. those mentioned by Gauld, 1991). Idiobiont parasitoids are clearly dominating, with the genus *Neotheronia* being especially abundant in the Neotropics.

LATITUDINAL SPECIES-RICHNESS GRADIENT.—Our results lend no support to the anomalous latitudinal species-richness gradient that was originally proposed by Owen & Owen (1974), at least for the subfamilies Pimplinae and Rhyssinae. We found a lot of variation in species richness within latitudes but variable sampling effort makes the results difficult to interpret. If anything, the observed maxima of local species richness follow the usual species-richness gradient, i.e. the observed numbers of species peak in the tropics and decrease towards the poles. Owen & Owen (1974) examined samples collected in Northern Europe and in the Afrotropical region. They observed that "a quite extraordinary number of species was found once" in their samples, which suggests that the parasitoid wasp communities were only superficially sampled. Janzen & Pond (1975) and Janzen *et al*. (1976) agreed with the phenomenon of reverse latitudinal gradient but did not demonstrate that their sampling efforts were representative enough to support such broad generalizations. As a result, the phenomenon was popularized although it was based on data obtained from only a handful of study localities that were not even distributed along a proper latitudinal gradient.

In our northern Peruvian site, two years of sampling with several Malaise traps was insufficient to obtain a complete representation of the species in any one locality. Such an

outcome is expected when sampling hyperdiverse organisms (Colwell & Coddington, 1994). Together with the results from all the parasitoid studies analysed here, this leads us to agree with the proposal that the main reason why low latitudes have been thought to be relatively species-poor for ichneumonids is insufficient sampling effort (e. g. Hespenheide, 1978; Morrison *et al*., 1979; Sime & Brower 1998; Sääksjärvi *et al*., 2004; Santos & Quicke, 2011).

LOCAL SPECIES COMPOSITION IN PERUVIAN AMAZONIA.—The Malaise traps differed considerably in how many species they captured (Fig. 2). This was not related to habitat type in any obvious way, although in Allpahuayo-Mishana there was a weak tendency for traps in white sand forests to capture fewer species per unit time than traps in the other kinds of forest did (Fig. 4B). This would agree with earlier reports that white sand forests have fewer plant and animal species than other non-inundated forest types do (Anderson, 1981; Tuomisto & Ruokolainen, 1994). This, together with the simpler forest structure, may lead to this habitat type providing fewer niches for parasitoids. The relatively open canopy in white sand forests also makes them rather sunny and possibly dry, which is thought to be unfavourable for ichneumonids (Gauld, 1991). However, this cannot be the only explanation since secondary forest had higher species-richness than the other habitats. This parallels results from Brazilian Amazonia, where moth species richness in secondary forest was consistently higher than in primary forest (Barlow *et al*., 2007). The degree of dominance was also high in secondary forests: diversity (which takes species abundances into account) was clearly lower in secondary forests than in old-growth forests on loamy soils (Fig 5B), although there appeared to be no obvious difference in species richness (Fig 5A).

It is noteworthy that half of the Pimplinae and Rhyssinae species that were observed in Los Amigos were not found in Allpahuayo-Mishana, and less than 20% of the observed species were shared between the two sites. This may partly be due to undersampling, as the species

accumulation curves indicate that part of the species pools remained unsampled in both areas. However, it is likely that there is also a real difference between their ichneumonid faunas, which could be due to at least two causes. Firstly, the two sites are more than 1000 km apart, and there might already be biogeographical differences between their regional species pools. Secondly, the habitat types sampled in the two sites were different: sampling in Los Amigos was mostly in floodplain forests, whereas sampling in Allpahuayo-Mishana was in non-inundated forests. Therefore, any specialists of floodplain forests would have been missed in Allpahuayo-Mishana, even though they might exist in the general area. Conversely, specialists of white sand forests could not have been observed in Los Amigos, as such forests are not known to occur in the area. Such possibilities open up interesting questions about the ecology and biogeography of ichneumonid wasps.

SAMPLING EFFORT.—There was considerable variation among individual Malaise traps in how many specimens and species they captured per unit time. Indeed, it is obvious that the precise placement of a Malaise trap may have a considerable impact on how many insects it captures. On the other hand, the number of individuals captured was a good predictor of the number of species observed (Fig. 5A). This suggests that when the interest is in comparing species-richness or diversity values among sites, it is more important to ensure comparable sampling efficiency (number of individuals captured) than comparable sampling effort (time spent sampling).

The total sampling effort in all our field localities (the red dots in Fig. 1) was 628 MTM, of which 257 MTM was focused on Peruvian Amazonia. The species accumulation curves for the different habitats showed that our sampling was nowhere near complete (Fig. 3–4; Colwell & Coddington, 1994). This was true even for the most intensively studied habitat

type, namely white-sand forest, which was sampled by 93 MTM in Allpahuayo-Mishana. Indeed, species-richness was still expected to increase by 10-30% if sampling were continued (Fig. 4). This parallels earlier results from Costa Rica, where only 32 Pimplinae and Rhyssinae species were known before the study of Gauld (1991). After extensive sampling programs this number increased to a total of 195 species (Gauld *et al*., 1998). Likewise, sampling conducted over a decade increased the number of Pimplinae species known from Vietnam from 39 to 122 (Pham 2013). In both of these tropical countries, it took several years of sampling to produce a significant increase in the species richness. In Peru, a total of 128 Pimplinae and Rhyssinae species were recorded here from the two Amazonian localities, but more can be expected.

Most studies on parasitoid wasps have been carried out in the northern hemisphere. This has left the southern hemisphere poorly known, including the recognised diversity hotspots there (Orme *et al*., 2005). This situation may also be one reason for the fact that the known ichneumonid genera are heavily concentrated in the northern hemisphere (Quicke, 2012). In addition, most studies have focused on lowlands (Table S1), so information from mid and high altitude areas is sparse. Both of these biases in sampling need to be considered when studying the distributional patterns of ichneumonids.

Morrison *et al*., (1979) lamented that the sampling effort was insufficient in tropical and temperate regions to provide a clear understanding of species-richness patterns of these parasitoids, and we suggest that the situation has remained similar to the present day. Species accumulation curves from our intensively sampled Peruvian sites suggest that most of the study localities for which we have found published data (Table S1) are still too superficially sampled to allow a reliable estimation of local ichneumonid species richness to be made.

Although the two Peruvian Amazonian localities seem to be the most species-rich sites in the world for the subfamilies Pimplinae and Rhyssinae, this may just be a consequence of the extensive sampling effort in them. The situation may well change when other sites become more intensively sampled. However, in the light of the currently available data, it is plausible that the species richness of Ichneumonidae (or at least Pimplinae and Rhyssinae) follows the usual latitudinal trend of highest local diversity in the lowland tropics.

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FIGURES AND TABLES

Fig. 1 Sites with information on Pimplinae and Rhyssinae species richness. Red circles represent localities inventoried for this study, blue circles localities for which data were compiled from the literature.

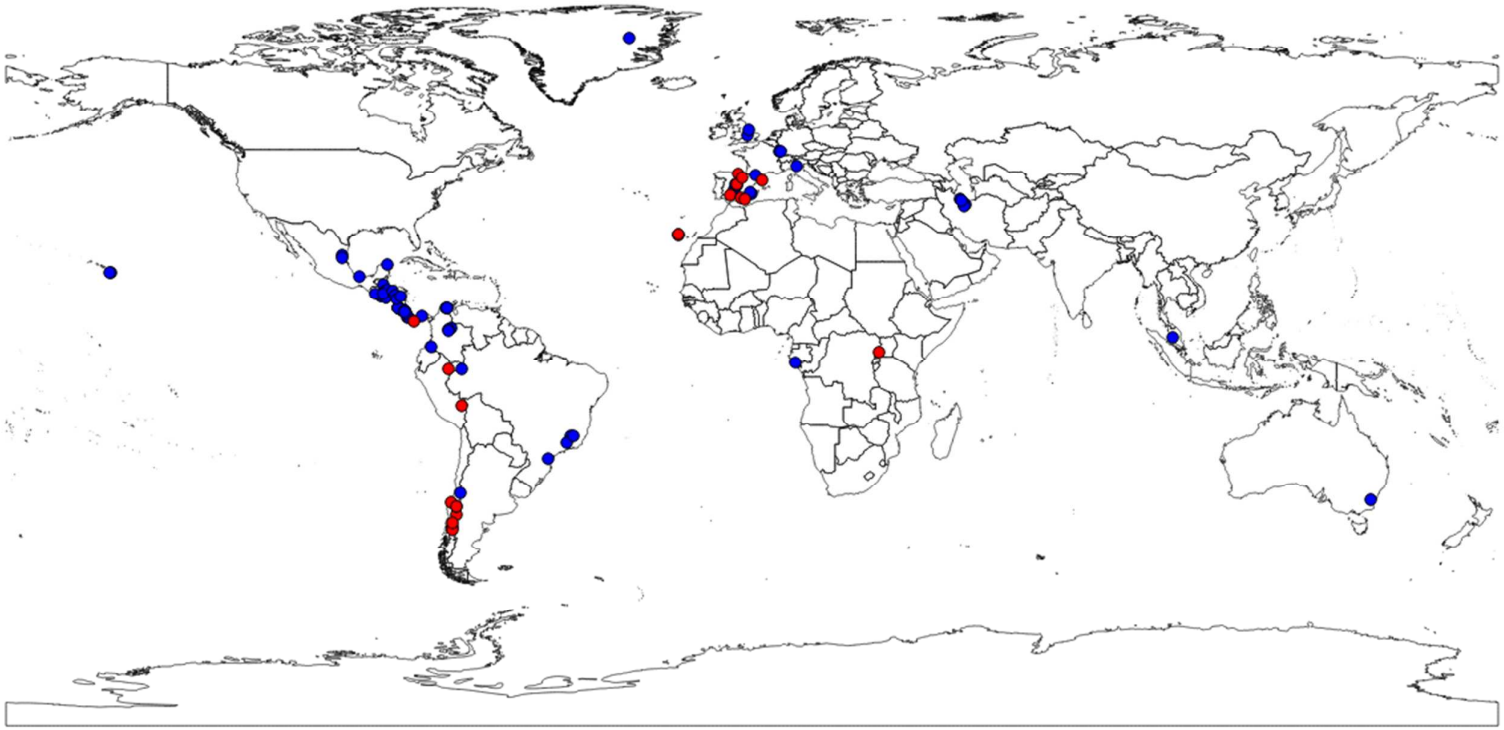

Figure 2. Accumulation of individuals (A) and species (B, C) as a function of sampling duration (A, B) and the number of individuals captured (C) in Malaise traps in Peruvian Amazonia. Each line corresponds to one trap and displays the observed accumulation of individuals or species during the entire operational period. A-M refers to Allpahuayo-Mishana (northern Peru), LA to Los Amigos (southern Peru).

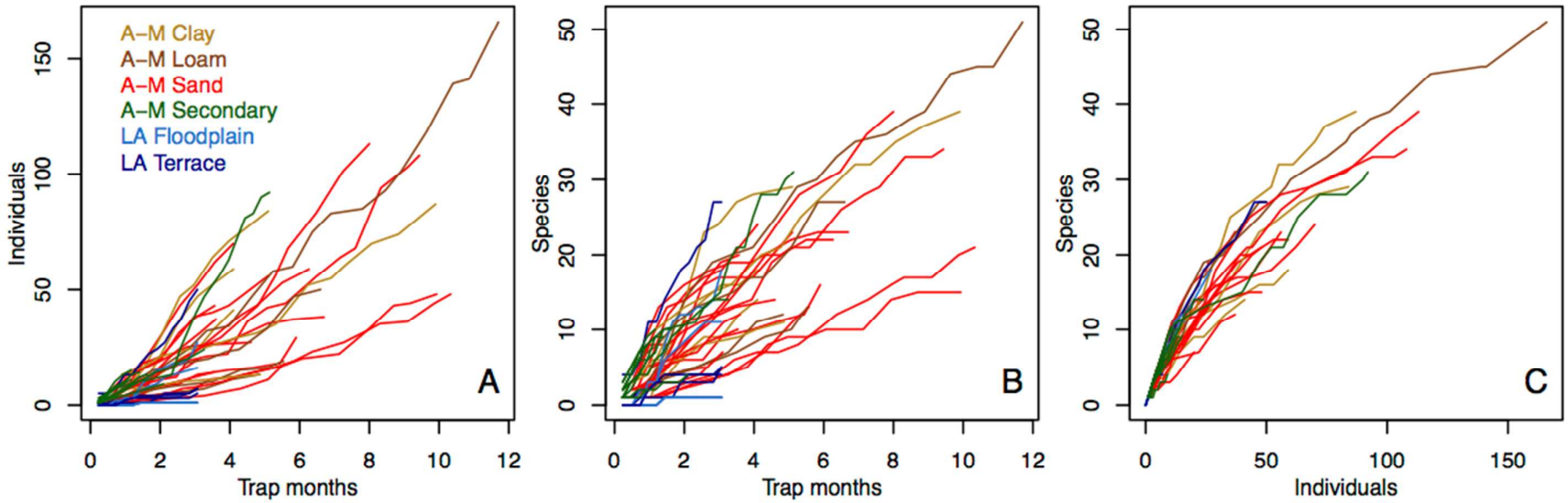

Figure 3. Estimated number (A) and percentage (B) of additional Pimplinae and Rhyssinae species expected if more individuals could have been added to samples currently available from Peruvian Amazonia. Each circle corresponds to the total catch in a number of original 1-2-week samples that were combined randomly but always within the same habitat type. A-M refers to Allpahuayo-Mishana (northern Peru), LA to Los Amigos (southern Peru).

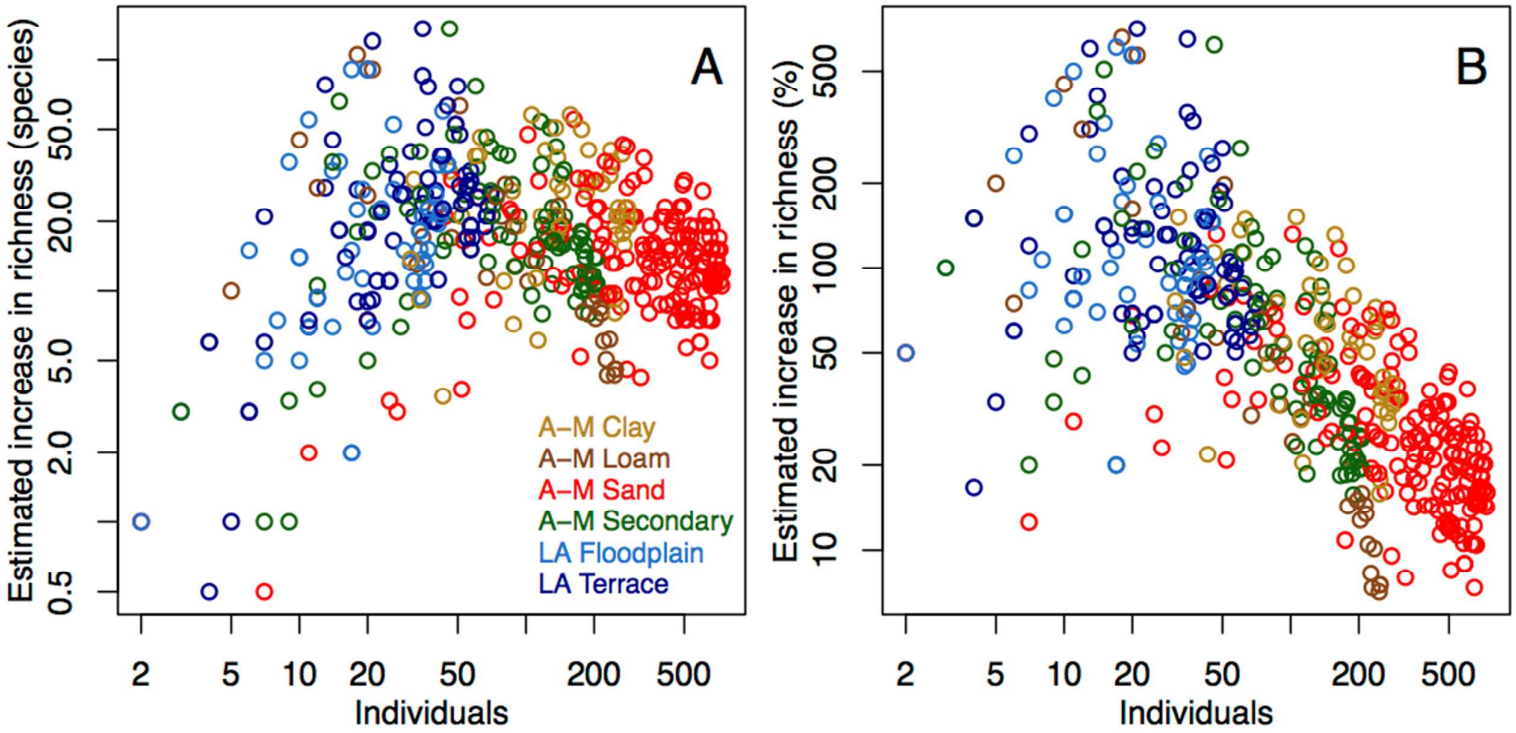

Figure 4. Accumulation of Pimplinae and Rhyssinae individuals (A) and species (B) as a function of sampling effort (Malaise trap months) in Peruvian Amazonia (A-M and LA) and in other parts of the world (Literature). Symbols in grey correspond to samples that only reported Pimplinae. Open circles correspond to lowland sites (<1000 m elevation) and closed circles to montane sites (>1000 m elevation). Circle size is proportional to absolute value of latitude. For Allpahuayo-Mishana and Los Amigos (A-M and LA, respectively), each symbol corresponds to a combination of randomly chosen 1-2-week samples from the same habitat type. Some literature sites present in B are missing from A because they did not report number of individuals.

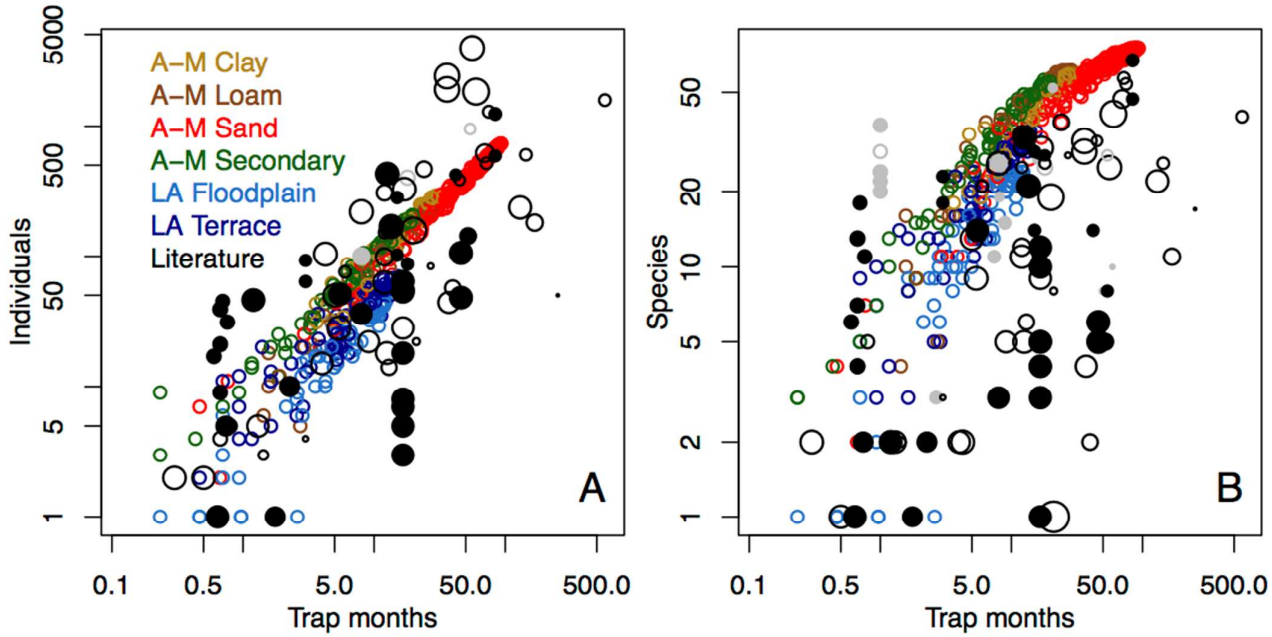

Figure 5. Accumulation of species richness (A) and diversity (B, C) of Pimplinae and Rhyssinae wasps as a function of the number of individuals captured in Malaise traps in Peruvian Amazonia (A-M and LA) and in other parts of the world (Literature). Diversity at q=1 equals the exponential of the Shannon index and diversity at q=2 the reciprocal of the Simpson index. Second-order polynomial regression lines are shown in (A) separately for our Peruvian data (black) and for data from other parts of the world (grey). For detailed explanation of the symbols, see Fig. 4.

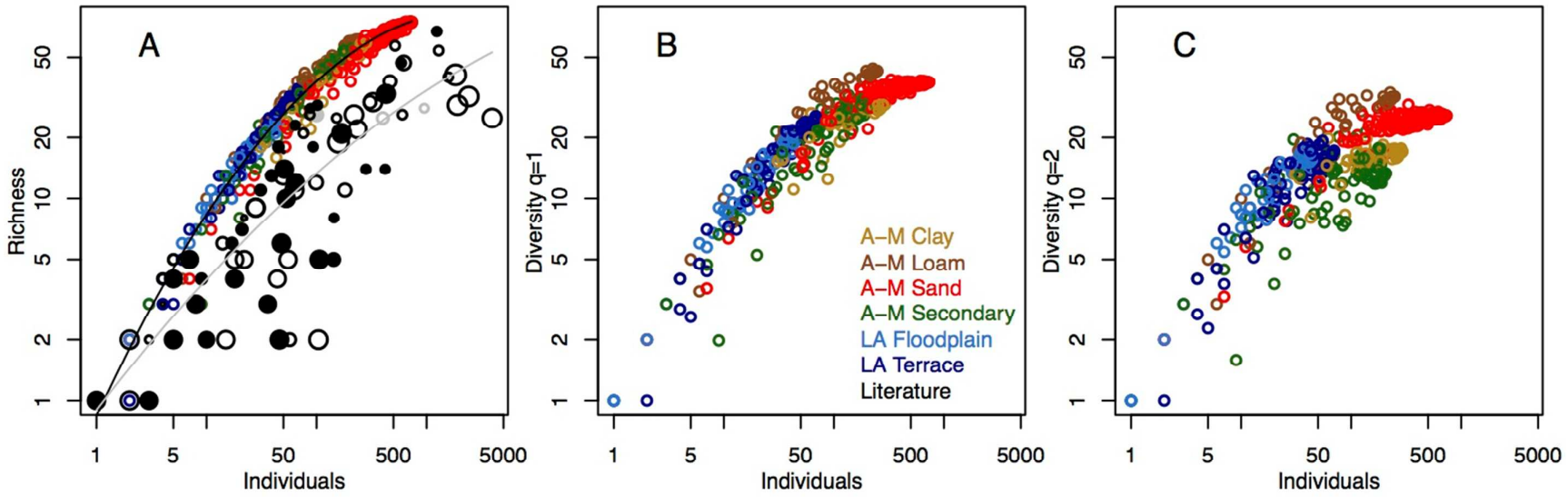

Figure 6. (A) Number of Pimplinae and Rhyssinae species in samples obtained at different latitudes with circle sizes reflecting sampling effort (Malaise trap months). Open symbols correspond to lowland sites (<1000 m) and closed symbols to montane sites (>1000 m). (B) The residuals from a second-order polynomial regression of number of species against number of individuals, both logarithmically transformed with log base 10, plotted against absolute latitude (a residual of -1.0 indicates that the observed number of species is one-tenth of what would be expected, given the number of individuals). Two regression lines are shown to test separately for latitudinal trends in lowland and montane sites (cut-off elevation 1000 m). Symbol size reflects elevation, with montane sites highlighted with a slightly thicker line. (C) Like (B), but residuals plotted against elevation, and regressions are given separately for tropical and non-tropical sites (cut-off latitude 25 degrees). Symbol size reflects absolute latitude. In all three panels, coloured symbols correspond to a random subsample of the data from our Peruvian sites; colour scheme is the same as in Fig. 4. Each of the other study localities shown in Table S1 is indicated with a black or grey symbol (for studies reporting both Pimplinae and Rhyssinae vs only Pimplinae, respectively).

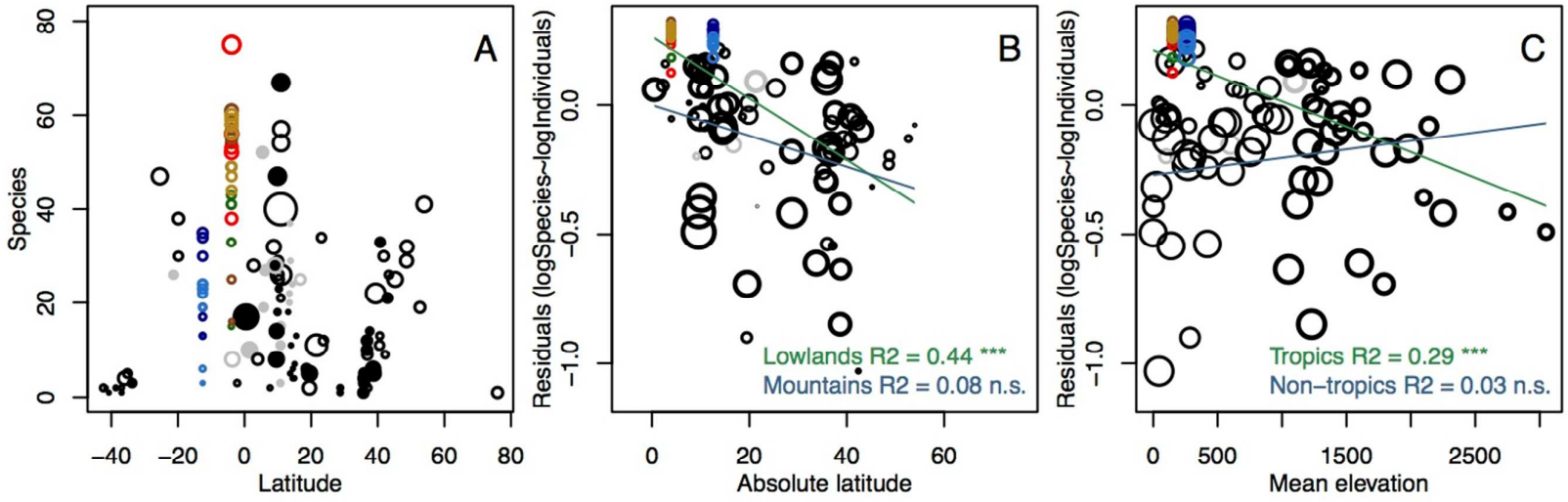

Table 1. Summary of the sampling methods and sampling effort in ichneumonid inventories in two Peruvian Amazonian sites.

Site	**Allpahuayo-Mishana**			**Los Amigos**
Collection year	1998	2000	2011	2008
Malaise sampling	41MTM	144MTM	45MTM	27MTM
Yellow pan trap	_	_	76.7 traps month	_
Hand netting	_	_	92 hours	52 hours
Larval rearing	_	_	3298	_
Pupal rearing	_	_	113	_

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1 Species-richness of Pimplinae and Rhyssinae in 97 sites sampled with Malaise traps around the world. MTM: Malaise trap months; C.T: Caldera de Taburiente; S.N.: Sierra Nevada; P.N.: Parque Nacional; R.N. Reserva Nacional; *: Studies that reported only Pimplinae and may not include Rhyssinae.

Country	Locality	Species	Individuals	MTM	Indiv./MTM	Elevation	Latitude	Longitude	Reference

						(m)			
Australia	Ginninderra	5	22	9.1	0.55	588-615	-35.15	149.03	Steinbauer *et al*., (2006)
Belize	Las Cuevas	25	400	18	22.2	600	16.73	-88.98	*Bartlett *et al*., (1999)
Brazil	Boqueirão	26	100	8	12.5	1100	-21.33	-44.98	*Tanque & Frieiro 2011
Brazil	Capão da Imbuia	47	620	70	8.9	900	-25.42	-49.23	Kumagai & Graf 2002
Brazil	Belo Horizonte	30	306	12	25.5	850	-19.87	-43.97	Kumagai 2002
Brazil	Santa Barbara	38	465	24	19.3	770-800	-19.88	-43.37	Tanque *et al*., 2009
Chile	Alerce Andino	2	2	0.3	6.7	129-141	-41.58	-72.58	In this study
Chile	Conguillio	2	46	1.2	38.3	1195-1264	-38.63	-71.65	In this study
Chile	Huinay, Comau Fjord	2	104	4.25	24.47	45	-42.38	-72.42	In this study
Chile	Ñuble	2	5	1.3	3.8	754-765	-36.93	-71.55	In this study
Chile	Puyehue	1	2	0.5	4	367-558	-40.73	-72.32	In this study
Chile	R. N. Les Queules	4	44	37.17	1.18	420	-35.99	-72.71	In this study
Chile	Valle las Trancas	1	1	0.64	1.6	1220	-36.9	-71.48	In this study
Chile	Rio Clarillo	3	36	8	4.5	1600	-33.75	-70.42	Porter, 1997

Colombia	Amacayacu	8	_	50	_	150-210	-3.68	-70.25	* Sharkey 2006
Colombia	Iguaque high	27	_	15.83	_	3300-3420	6.25	-72.71	* Sharkey 2006
Colombia	Iguaque low	19	_	8.1	_	2600	5.71	-73.46	* Sharkey 2006
Colombia	Iguaque mid	52	_	20.7	_	2820-2920	5.41	-73.45	* Sharkey 2006
Colombia	Planada	10	_	59	_	1800-1930	1.5	-77.53	* Sharkey 2006
Colombia	S. N. de Santa Marta high	11	_	7.4	_	2300-2500	10.8	-73.65	* Sharkey 2006
Colombia	S. N. de Santa Marta low	3	_	2.67	_	1500-1700	10.76	-73.91	* Sharkey 2006
Colombia	S. N. de Santa Marta mid	15	_	8.93	_	2200-2220	10.82	-73.88	* Sharkey 2006
Costa Rica	16 km W Guapiles	26	87	18	4.8	400	10.15	-83.92	Gaston & Gauld 1993
Costa Rica	Casa Maritza	54	1289	75	17.2	600-650	10.95	-85.5	Gaston & Gauld 1993
Costa Rica	Cerro de Hacha	26	602	144	4.2	300-400	11	-85.55	Gaston & Gauld 1993
Costa Rica	Cerro de la Muerte	14	420	42	10	2700-2800	9.63	-83.8	Gaston & Gauld 1993
Costa Rica	Estacion Cacao	67	1239	84	14.8	1000-1100	10.93	-85.47	Gaston & Gauld 1993
Costa Rica	Estacion Pitilla	57	517	72	7.2	600-700	11	-85.43	Gaston & Gauld 1993
Costa Rica	Finca San Gabriel	21	76	6	12.7	650-700	10.88	-85.4	Gaston & Gauld 1993

Costa Rica	Golfo Dulce Forest	32	383	45	8.5	100-200	8.75	-83.33	Gaston & Gauld 1993
Costa Rica	La Selva	25	152	12	12.7	50-75	10.43	-84.02	Gaston & Gauld 1993
Costa Rica	Monteverde	23	64	3	21.3	1300-1350	10.3	-84.8	Gaston & Gauld 1993
Costa Rica	Rio Agres	18	93	3	31	1500	9.88	-84.13	Gaston & Gauld 1993
Costa Rica	San Antonio de Escazu	47	590	84	7	1300	9.9	-84.13	Gaston & Gauld 1993
Costa Rica	Santa Rosa	40	1579	576	2.7	250-300	10.85	-85.62	Gaston & Gauld 1993
Costa Rica	San Vito	28	88	18	4.9	1200	8.8	-82.97	Gaston & Gauld 1993
Costa Rica	Vara Blanca	14	281	15	18.7	2100	10.15	-84.13	Gaston & Gauld 1993
Costa Rica	Villa Mills	8	144	54	2.7	3000-3100	9.57	-83.72	Gaston & Gauld 1993
Costa Rica	Zurqui de Moravia	29	102	15	6.8	1600	10.07	-84	Gaston & Gauld 1993
El Salvador	Ahuachapan	29	_	1	_	660-800	13.8	-89.85	* Gauld *et al*., 2002
El Salvador	La Libertad	37	_	1	_	1000	13.65	-89.37	* Gauld *et al*., 2002
El Salvador	San Vicente	22	_	1	_	1100	13.47	-88.52	* Gauld *et al*., 2002
El Salvador	Santa Ana	24	_	1	_	1450	14.37	-89.27	* Gauld *et al*., 2002
El Salvador	Usulutan	20	_	1	_	1480	13.47	-88.52	* Gauld *et al*., 2002

France	Bezange à bois mort	32	2412	36	67	260	48.75	6.45	Robert 2011
France	Parroy à bois mort	29	1909	36	53	270	48.63	6.63	Robert 2011
France	Gar-Cagire	21	169	13.5	12.5	1328-1500	42.95	0.7	Rome 2006
Gabon	Monts Doudou	3	4	3	1.3	110-630	-2.22	10.38	Van Noort 2004
Greenland	Northeast National Park	1	_	21	_	598-791	75.95	-29.93	Várkonyi & Roslin, 2013
Guatemala	Atlitan	6	17	0.6	28.3	1575-1685	14.52	-91.19	Veijalainen *et al*., 2014
Guatemala	Montaña Chiclera	4	4	0.67	6	210-245	14.95	-88.87	Veijalainen *et al*., 2014
Honduras	Cusuco	13	39	0.67	58.2	1210-1260	15.55	-88.24	Veijalainen *et al*., 2014
Honduras	Guisayote	4	9	0.67	13.4	2090-2190	14.45	-89.07	Veijalainen *et al*., 2014
Honduras	La Muralla	7	21	0.67	31.3	1410-1530	15.07	-86.74	Veijalainen *et al*., 2014
Iran	Arangeh	4	5	16.6	0.3	1891	35.92	51.08	Mohammadi *et al*., 2013
Iran	Astaneh-e-Ashrafieh	5	55	16.6	3.3	-1	37.36	49.95	Mohammadi *et al*., 2013
Iran	Ghazichak	10	53	16.6	3.2	1803	36.75	50.32	Mohammadi *et al*., 2013
Iran	Karaj	4	18	16.6	1.1	1278	35.77	50.93	Mohammadi *et al*., 2013

Iran	Orkom	12	64	16.6	3.9	1201	36.75	50.3	Mohammadi *et al*., 2013
Iran	Sarziarat	3	8	16.6	0.5	1980	35.92	51.1	Mohammadi *et al*., 2013
Iran	Shahrestanak	5	7	16.6	0.4	2305	35.95	51.37	Mohammadi *et al*., 2013
Iran	Shahryar	1	3	16.6	0.2	1168	35.67	50.93	Mohammadi *et al*., 2013
Iran	Ziaz	9	28	16.6	1.7	537	36.87	50.22	Mohammadi *et al*., 2013
Italy	Bosco della Fontana	25	3945	56	70.4	25	45.2	10.73	Di Giovanni *et al*., 2014
Malaysia	Langat basin	28	84	27	3.1	50-200	2.73	101.44	Idris & Hainidah, 2003
Malaysia	Sungkai	8	22	21	1	60	3.97	101.25	Idris & Kee, 2002
Mexico	Ria Lagartos	11	181	168	1.1	0-4	21.6	-88.17	Gonzalez & Bordera, 2012
Mexico	Cañon del Novillo	12	99	12	8.3	420	23.68	-99.2	Perez-Urbina *et al*., 2010
Mexico	Rancho Santa Elena	13	263	12	21.9	750	23.62	-99.2	Castillo *et al*., 2014
Mexico	Los Tuxtlas	6	14	13	1.07	76-159	18.58	-95.05	Ruiz-Guerra *et al*., 2013
Nicaragua	Cerro Jesus	11	31	0.76	40.8	1440-1780	13.97	-86.18	Veijalainen *et al*., 2014
Nicaragua	Datanlí-El Diablo	18	45	0.7	64.3	1330-1440	13.12	-85.87	Veijalainen *et al*., 2014

Nicaragua	Saslaya low	5	5	0.8	6.3	290-370	13.73	-84.98	Veijalainen *et al*., 2014
Panama	Barro Colorado	28	952	54	17.6	100	9.15	-79.85	*Bartlett *et al*., 1999
Panama	P. N. Isla de Coiba	2	3	1.43	2.1	40	7.63	-81.73	In this study
Peru	Allpahuayo-Mishana	105	1597	240	6.7	110-180	-3.95	-73.43	In this study
Peru	Los Amigos	51	121	27	4.5	260	-12.57	-70.08	In this study
Spain	El Cabril	5	18	12.5	1.44	300	38.05	-5.42	In this study
Spain	Roblehondo (Cazorla)	14	51	5.5	9.27	1280	37.95	-2.88	In this study
Spain	Hoyo de Manzanares	13	50	5	10	970	40.62	-3.91	In this study
Spain	Llueva	26	219	8	27.38	100	43.33	-3.55	In this study
Spain	Mirambell	30	326	17	19.18	900	41.8	2.19	In this study
Spain	Mojácar	2	15	4	3.75	137	37.12	-1.85	In this study
Spain	San Roque de Riomiera	9	28	5.4	5.19	570	43.23	-2.71	In this study
Spain	El Pardo	11	63	12	5.25	750	40.54	-3.73	In this study
Spain	Carrasqueta	6	48	46	1.04	940-1300	38.6	-0.48	Mazon *et al*., 2009
Spain	Mariola	5	106	46	2.3	900-1200	38.75	-0.5	Mazon *et al*., 2009

Spain	El Ventorrillo	33	428	12.6	34	1450	40.75	-4.02	Nieves-Aldrey *et al.*,2003
Spain	Cabañeros	22	236	130	1.8	800	39.37	-4.48	Mazon *et al.*, 2014
Spain (C. Islands)	Isla de la Palma C.T. Barranco de Las Traves	1	1	1.76	0.57	1050	28.72	-17.89	In this study
Spain (C. Islands)	Isla de la Palma C.T. Roque de la Cumbrecita	2	5	0.74	6.75	1297-1377	28.7	-17.86	In this study
Spain (C. Islands)	Isla de la Palma C.T. Roque de los Muchachos	2	10	2.27	4.4	2250	28.75	-17.88	In this study
Uganda	Kibale	17	50	252	0.2	1240-1375	0.48	30.38	In this study
UK	York	41	1836	60	30.6	15	53.95	-1.07	Mayhew *et al.*, 2009
UK	Leicester	19	158	20	7.9	120	52.67	-1.18	Owen *et al.*, 1981

USA (Hawaii)	Bryson´s	2	57	39.8	1.4	285	19.45	-154.92	Peck *et al*., 2008
USA (Hawaii)	Solomon´s Waterhole	5	143	52.1	2.7	1792	19.53	-155.32	Peck *et al*., 2008

Table S2 Abundance, species richness and functional type of the Pimplinae and Rhyssinae genera found in the Peruvian localities Allpahuayo-Mishana and Los Amigos. The functional types follow Gauld (1991) and Sääksjärvi et al. (2004) and are: IDC = idiobiont parasitoids of deeply concealed hosts (hosts located e.g. within wood); IWC = idiobiont parasitoids of weakly concealed hosts (exposed hosts or hosts within e.g. leaf rolls); IES / Pseudo = idiobiont ectoparasitoids of spiders, or pseudoparasitoids of spider egg sacs; and 4) KES = koinobiont ectoparasitoids of spiders.

		Allpahuayo-Mishana		**Los Amigos**		
Subfamily	**Genus**	**Individuals**	**Species**	**Individuals**	**Species**	**Functional type**
Rhyssinae	*Epirhyssa*	81	13	15	9	IDC
Pimplinae	*Anastelgis*	11	1	5	1	IDC
Pimplinae	*Dolichomitus*	44	4	12	5	IDC
Pimplinae	*Amazopimpla*	9	2	1	1	IWC
Pimplinae	*Clydonium*	1	1	_	_	IWC

Pimplinae	*Zonopimpla*	3	1	3	3	IWC
Pimplinae	*Neotheronia*	881	41	51	20	IWC
Pimplinae	*Nomosphecia*	10	3	_	_	IWC
Pimplinae	*Pimpla*	95	1	14	1	IWC
Pimplinae	*Xanthopimpla*	137	6	3	2	IWC
Pimplinae	*Zaglyptus*	39	3	2	1	IES / Pseudo
Pimplinae	*Tromatobia*	_	_	2	1	IES / Pseudo
Pimplinae	*Acrotaphus*	103	8	2	1	KES
Pimplinae	*Hymenoepimecis*	146	13	8	5	KES
Pimplinae	*Polysphincta*	15	3	_	_	KES
Pimplinae	*Ticapimpla*	12	3	_	_	KES
Pimplinae	*Zatypota*	10	2	_	_	KES
Pimplinae	genus unknown	_	_	3	1	KES
Total		1597	105	121	51	